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# Current views on chelicerate phylogeny—a tribute to Peter Weygoldt

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## **ABSTRACT**

Peter Weygoldt pioneered studies of arachnid phylogeny by providing the first synapomorphy scheme to underpin inter-ordinal relationships. Since this seminal work, arachnid relationships have been evaluated using morphological characters of extant and fossil taxa as well as multiple generations of molecular sequence data. While nearly all datasets agree on the monophyly of Tetrapulmonata, and modern analyses of molecules and novel morphological and genomic data support Arachnopulmonata (a sister group relationship of Scorpiones to Tetrapulmonata), the relationships of the apulmonate arachnid orders remain largely unresolved. Three threads may allow us to resolve the recalcitrant phylogeny of arachnids: the careful evaluation of large amounts of molecular data; novel techniques grounded in comparative morphology and evolutionary developmental biology, which add improved homology statements and explain the transition between character states; and new fossil discoveries, which continue to incorporate relevant novel data to the discussion of the relationships among the arachnid orders.

## **1. Introduction**

Professor Peter Weygoldt, one of the most influential workers on arachnid systematics, produced the first explicit synapomorphy scheme and cladistic analysis of chelicerate

relationships based on morphological data (Weygoldt and Paulus, 1979a, b; see also Weygoldt, 1980). His views persisted until the end of the 20<sup>th</sup> century, when the molecular influence on arachnid systematics was still not mainstream (Weygoldt, 1998; Weygoldt, 1999). Since then, arachnid systematists have continued to support monophyly of Arachnida. A sister group relationship of Scorpiones to Lipoctena (the non-scorpion arachnids) was also mainstream, along with the monophyly of Acari, among other views, but these are now largely rejected by most authors. Lipoctena were split into two main groups, Megoperculata (= the modern Tetrapulmonata) and Apulmonata (the non-pulmonate arachnids), a view earlier proposed by Firstman (1973), and to some extent, endorsed by recent molecular analyses. Weygoldt and Paulus' cladogram (Fig. 1) constituted the basis of modern chelicerate systematics and provided the first classification integrating multiple character systems and explicit synapomorphies. Their synapomorphy scheme was subsequently incorporated into follow-up data matrices and cladistic analyses of arachnid and arthropod relationships (e.g., Shultz, 1990; Wheeler and Hayashi, 1998; Edgecombe et al., 2000; Dunlop and Braddy, 2001; Giribet et al., 2002; Pollitt et al., 2003; Shultz, 2007; Garwood et al., 2014; Garwood et al., 2016; Garwood et al., 2017), some of which combined morphology with molecules in total evidence analyses (e.g., Wheeler and Hayashi, 1998; Edgecombe et al., 2000; Giribet et al., 2002).

In this review I present my views on the current understanding of chelicerate phylogeny in light of Weygoldt and Paulus' (1979b) cladogram, contrasting it with recent, often molecularly-driven views on chelicerate evolution.

## **2. Chelicerate phylogeny—a historical account**

Satisfactorily resolving the phylogenetic tree of Chelicerata has been among the most difficult systematic problems in Arthropoda since the proposal of the first explicit hypothesis of relationships by Pocock (1893). Traditionally divided into three major extant lineages, Pycnogonida (sea spiders), Xiphosura (horseshoe crabs), and Arachnida (spiders, scorpions, harvestmen, mites, etc.), plus several extinct ones (e.g., Eurypterida, Chasmataspida), the interrelationships among these three main extant

clades (and the fossils) remain unsettled. The monophyly and relationships among the arachnid orders<sup>1</sup> remain even more fluid, if possible. These relationships have been constantly debated based on morphology (e.g., Weygoldt and Paulus, 1979b; Shultz, 1990; Wheeler and Hayashi, 1998; Giribet et al., 2002; Pollitt et al., 2003; Giribet et al., 2005; Shultz, 2007; Legg et al., 2013; Garwood and Dunlop, 2014; Garwood et al., 2016; Garwood et al., 2017) and have remained frustratingly unstable and poorly supported based on molecules (e.g., Wheeler and Hayashi, 1998; Giribet and Ribera, 2000; Giribet et al., 2002; Mallatt and Giribet, 2006; Masta et al., 2009; Regier et al., 2010; Ovchinnikov and Masta, 2012; Sharma et al., 2014a; Pepato and Klimov, 2015). Few results are thus supported across methods or classes of data, even after using large amounts of molecular data (Regier et al., 2010; Sharma et al., 2014a). These latter studies used dozens to thousands of genes but were only able to recover Arachnida under particular conditions, and not consistently. Nevertheless, cladistic analyses of morphological data consistently support the monophyly of Arachnida (Weygoldt and Paulus, 1979b; Wheeler and Hayashi, 1998; Giribet et al., 2002; Giribet et al., 2005; Shultz, 2007; Legg et al., 2013; Garwood and Dunlop, 2014), as do most combined analyses of molecular and morphological datasets (Wheeler and Hayashi, 1998; Edgecombe et al., 2000; Giribet et al., 2002; Giribet et al., 2005), so this incongruence between molecular and morphological data has puzzled systematists for almost three decades.

Nearly all data and analyses agree now that Pycnogonida and Euchelicerata are sister taxa, and that Euchelicerata is monophyletic, even when multiple fossils are included (Legg et al., 2013). This has been however contradicted by two recent phylogenetic analyses placing Pycnogonida as sister group to Arachnida, with Xiphosura and several related fossils being more basal (Garwood and Dunlop, 2014; Garwood et al., 2017), a result that is probably due to the long branches of pycnogonids and appears contradicted by virtually all recent analyses of molecular data (but see the mitochondrial gene analyses of Ovchinnikov and Masta, 2012). Indeed, some analyses of mitochondrial data place Pycnogonida deeply nested within Arachnida (Ovchinnikov and Masta, 2012), but mitochondrial data analyses also fail to recover the only group supported virtually by all morphological and molecular analyses—Tetrapulmonata (Masta et al., 2009; Masta, 2010; Ovchinnikov and Masta, 2012).

In addition to the recalcitrant problem of the monophyly of Arachnida, the interrelationships of its orders have remained in flux and few aspects are shared even among morphological proposals (Weygoldt and Paulus, 1979b; Shultz, 1990; Wheeler and Hayashi, 1998; Giribet et al., 2002; Giribet et

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<sup>1</sup> While some advocate for rankless classification systems, I follow my explicit principles (see Giribet et al., 2016) of using ranks as conventional non-comparable evolutionary units (e.g., an order can be sister group to all other orders), since everyone understands what an arachnid order refers to (perhaps except for the case of the acarine orders).

al., 2005; Shultz, 2007; Garwood and Dunlop, 2014; Garwood et al., 2016; Garwood et al., 2017) (see Fig. 2). Tetrapulmonata (including the orders typically with four lungs, Araneae, Amblypygi, Uropygi<sup>2</sup> and Schizomida) is found almost universally, and it is equally supported in nearly all molecular analyses (see references above). A relationship of Tetrapulmonata to Scorpiones (a clade named Arachnopulmonata), a result endorsed by the homology of the book lungs of scorpions with the those of tetrapulmonates (Scholtz and Kamenz, 2006; Wirkner et al., 2013; Klußmann-Fricke and Wirkner, 2016), has been found in some molecular analyses (Regier et al., 2010; Sharma et al., 2014a), and was somehow recognized by early workers on arachnid phylogeny. I.e., Thorell (1876-1877: p. 86) placed Scorpiones as the sister group of Pedipalpi (although this clade was the sister group to Araneae + Opiliones, and Arachnida was not monophyletic). However, other early authors, including Pocock (1893), placed Scorpiones as the sister group to all other arachnids, a phylogenetic position that has prevailed, especially among paleontologists (e.g., Firstman, 1973; Weygoldt and Paulus, 1979b; Dunlop and Selden, 1998). Yet a myriad of other positions have been proposed for Scorpiones, including a sister group relationship to Eurypterida—not testable with molecular data—, Pseudoscorpiones, Opiliones, Solifugae, etc. (e.g., Shultz, 1990; Dunlop and Webster, 1999; Shultz, 2007; Garwood and Dunlop, 2014). While Tetrapulmonata, a clade based on a well-founded synapomorphy, has been corroborated with molecular data, another clade found in nearly all morphological phylogenies is one including Ricinulei and the acarine orders (currently six recognized orders), based on the presence of a hexapod larva, a unique character among arachnids. This clade, named Acaromorpha, is however refuted in nearly all molecular analyses, most of which also fail to support the monophyly of Acari. An accelerated rate of evolution in the acarine lineages may underpin the difficulties in resolving their precise phylogenetic position (Pepato et al., 2010; Sharma et al., 2014a; Pepato and Klimov, 2015), but it is now well understood that Acari divides into two clades, Acariformes and Parasitiformes + Opilioacariformes, and these may not be sister groups. Acariformes comprises the orders Trombidiiformes and Sacoptiformes; Parasitiformes includes the orders Ixodida, Mesostigmata and Holothyrida (Harvey et al., 2017). The relationships of Pseudoscorpiones, Palpigradi, Ricinulei, Solifugae, Opiliones and the two acarine clades are however poorly understood and they conflict in virtually every published analysis of arachnid relationships. Likewise, the position of some extinct arachnid orders is better understood than others, but often depends on the position of the extant ones.

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<sup>2</sup> I follow the convention of the International Society of Arachnology of using Thelyphonida as a clade including the orders Uropygi and Schizomida (see also Clouse et al., 2017).

I therefore do not think we can claim victory in having satisfactorily resolved arachnid relationships given the inconsistent results across morphological data matrices, across molecular data matrices, and across results from molecules and morphology. However, progress has been made in several areas of the tree since the seminal work of Weygoldt and Paulus, and some of these achievements are discussed below.

### **3. Arachnid monophyly**

While broadly accepted, the monophyly of the Arachnida has been disputed mostly by two sources of evidence: fossils and molecules. To my knowledge, no morphological cladistic analysis of extant arachnid relationships has challenged such monophyly. However, in cladistic analyses incorporating fossils, monophyly has been disputed in a few cases which supported a relationship of Scorpiones to Eurypterida and perhaps Xiphosura (see a discussion of hypotheses in Dunlop and Braddy, 2001). The often thought to be “more reliable” molecular data, have failed to recover arachnid monophyly in all but a very small minority of analyses.

Molecular data analyses that do not include morphology either fail to recover Arachnida (e.g., Wheeler and Hayashi, 1998; Giribet et al., 2002; Meusemann et al., 2010; Pepato et al., 2010; Regier et al., 2010; Rehm et al., 2011), or when Arachnida is recovered, it is poorly supported. Perhaps for this reason, some arthropod-wide phylogenetic analyses have included pycnogonids, xiphosurans, but a minimal representation of arachnids (e.g., Regier and Shultz, 2001; Regier et al., 2008). A few phylogenetic analyses of arthropod relationships have however recovered Arachnida with strong support, at least under some analytical conditions (Koenemann et al., 2010). Finally, a recent phylogenomic study of arachnid relationships explored the support for Arachnida under a variety of data matrices and found that depending on the analyzed dataset Arachnida could receive close to 100% bootstrap support (bs) or nearly 0% bs (Sharma et al., 2014a: figure 5).

The case of Sharma et al. (2014a) is particularly interesting because for the first time we could dissect where the signal for arachnid monophyly comes from. The authors binned sets of the more than 3,500 genes analyzed based on percent pairwise identity, and found that when adding genes from most to least conserved, Arachnida was recovered with 100% bs when adding 500 genes, but soon after this, by continuing adding more genes (more divergent ones), arachnid monophyly disappeared (see Fig. 3). This sequential concatenation of orthologs thus showed that Arachnida, unlike other groups that once

recovered continued to be found with total support after the addition of genes (i.e., Chelicerata, Euchelicerata, Tetrapulmonata, Pedipalpi, Arachnopulmonata; Fig. 3), was highly sensitive to the data analyzed. It is no coincidence that these are the groups typically recovered by nearly every molecular analysis. Arachnida, however, behaved more like other nodes that appeared and disappeared, but that their support peaked at different numbers of genes. As an example, Ricinulei and Solifugae formed a clade with nearly total support with about 500 genes, but a conflicting node of Ricinulei and Xiphosura achieved maximum support at 3,000 genes (Fig. 3). While the need of many highly divergent genes to obtain maximal support for a deep node may be an indication of some sort of systematic error, this study results in two corollaries: 1. Maximal support is not necessarily a good indicator of phylogenetic relationships; and perhaps more important, 2. Data matrices may not have the capacity to resolve all nodes in a phylogeny simultaneously. Therefore, we could ask whether we should use different matrices to resolve individual nodes, a discussion that is beyond the scope of this review.

#### **4. Scorpiones—Lipoctena or Arachnopulmonata?**

From the early days of arachnid systematics, Scorpiones have been considered the sister group to all other arachnids (= Lipoctena) (Pocock, 1893), and this relationship was endorsed by some modern analyses (Weygoldt and Paulus, 1979b). However, other positions have been proposed, including a sister group relationship to Eurypterida (see a discussion in Dunlop, 1998; Dunlop and Braddy, 2001); a basal arachnid group sister group to Opiliones (i.e., Stomothecata as sister group to remaining arachnids) (Shultz, 2007; with fossil taxa); derived arachnids within Dromopoda, either in Novogenuata (Shultz, 1990) or as sister group to Opiliones (i.e., Stomothecata as a derived arachnid clade) (Shultz, 2007; without fossils). Some of these hypotheses have been explicitly tested and, i.e., Garwood and Dunlop (2014) showed that Stomothecata was not particularly stable to the addition of further characters, or indeed to the addition of early fossils in each group which lack a stomotheca.

Nonetheless, early authors had recognized a putative clade of pulmonate arachids due to the similarities in their circulatory apparatus (Firstman, 1973), although some of the logic of these, not necessarily phylogenetic hypotheses, is difficult to interpret. Firstman's (1973) proposed "phyletic tree" showed monophyly of Pulmonata (later renamed Arachnopulmonata by Sharma et al., 2104, to distinguish it from the gastropod clade Pulmonata) and Apulmonata, as he also specified in his paper: "The Pulmonata and Apulmonata are both regarded as natural monophyletic categories". However, as it

was also typical at the time, other statements implied paraphyly of Merostomata, Scorpiones, and Pulmonata: “It is hypothesized that neoteny has been involved in the origin of arachnids from merostomes, and in the origin of apulmonate arachnids from pulmonates.”; “The Pulmonata is regarded as having emerged from the arachnid ancestors of modern scorpions.” Support for Arachnopulmonata is now found both in morphology (Scholtz and Kamenz, 2006; Wirkner et al., 2013; Klußmann-Fricke and Wirkner, 2016), and recent molecular analyses, including phylogenomic datasets (Koenemann et al., 2010; Regier et al., 2010; Sharma et al., 2014a), and a hemocyanin duplication (Sharma and Wheeler, 2014).

Unlike the case of arachnid monophyly, which continues to be poorly supported in molecular analyses, DNA and amino acid data seem to converge in a relationship of Scorpiones and Tetrapulmonata, thus rejecting the ideas of Lipoctena, Dromopoda, Novogenuata, and Stomothecata, to mention a few previously favored nodes. This should however not be perceived as a victory of molecules over morphology, as all of these hypotheses are supported by some sets of morphological characters, as is Arachnopulmonata, which has required nearly three decades of refinements in data acquisition and analyses before being supported with any confidence by molecular datasets. It is not outside the realm of possibilities that newer data and analyses may overturn the Arachnopulmonata hypothesis, but for the first time molecular data and detailed anatomical studies of circulatory and respiratory systems (held to be “convergent” between scorpions and tetrapulmonates for some years) are in agreement (Scholtz and Kamenz, 2006; Wirkner et al., 2013; Klußmann-Fricke and Wirkner, 2016). Genomic changes may also add support to clades that contain ancestral genome duplications, as are the cases of spiders and scorpions (Schwager et al., 2017). The study of these duplications may allow us to better understand the origins of novel morphological features through neofunctionalization, as in the case of the Hox genes in scorpions (Sharma et al., 2014b). Evodevo is also able to provide ultimate explanations to evolutionary transformations, as in the case from the 3-segmented to the 2-segmented chelicerae (Sharma et al., 2012). The application of a comparative framework to the evodevo approach is certainly a promising direction for understanding the evolution of arachnid morphology.

## **5. The position of the apulmonate orders**

While a small victory could be claimed with respect to Arachnopulmonata and its internal relationships (Tetrapulmonata, Pedipalpi, and even the position of the fossil Uraraneida), resolving the



relationships of theapulmonate orders has become frustratingly unrewarding. Pseudoscorpiones resemble Scorpiones in several aspects of their anatomy, most prominently on their unique pedipalps, and indeed, some authors consider them closely related, and some of the conserved genes in the analyses of Sharma et al. (2014a) place them together, or at least, with Arachnopulmonata. Likewise, Ricinulei and their putative fossil counterparts, Trigonotarbidia (Jones et al., 2014; Huang et al., 2018), are sometimes related to Tetrapulmonata, but sometimes Trigonotarbidia group with Arachnopulmonata while Ricinulei cluster with Acari (e.g., Huang et al., 2018). Acari are well known, as are pseudoscorpions, to have extraordinary rates of evolution when compared to other arachnids, making it extremely difficult to place them with any confidence (Pepato et al., 2010; Sharma et al., 2014a). Opiliones, Solifugae and Palpigradi are not better resolved, the latter group being extremely difficult to place phylogenetically, among other things due to the paucity of molecular data available until very recently (Regier et al., 2010; Giribet et al., 2014). A summary tree of what I believe to be the best-supported hypotheses of arachnid relationships is presented in Fig. 4.

Have we hit a wall attempting to resolve these relationships with confidence? Molecular analyses including a broad sample of arachnid diversity and more than a handful of loci remain scarce (Regier et al., 2010; Sharma et al., 2014a), and these two studies have a biased taxon representation, in addition to not having sufficient genes for resolving a tough phylogenetic question (Regier et al., 2010), or including a highly heterogeneous dataset (Sharma et al., 2014a). A new dataset including multiple species per arachnid order, better genomic/transcriptomic data, and a more balanced species distribution should be analyzed before giving up on the arachnid ordinal relationships. Additional genomic subsampling techniques are also a promising direction (Starrett et al., 2016), as they allow to add large number of species from specimens readily available in museum collections.

Morphology of course continues to be a source of reliable data to understand arachnid phylogeny, as it is ultimately the transformation of phenotypic traits that makes the phylogenetic enterprise interesting. As in the case of the circulatory system of Arachnopulmonata, many other relationships have alternatives. For example, Solifugae have been supported by many authors to be the sister group of Pseudoscorpiones, but a sister group to Acariformes (a clade now named Poecilophysidea) has been endorsed both by molecular analyses (Pepato et al., 2010) as well as sperm ultrastructure (Alberti and Peretti, 2002) and other anatomical characters, like the sejugal furrow (Dunlop et al., 2012).

Fossils are another obvious source of novel combinations of morphological characters, and new discoveries keep appearing every year. Among the most striking arachnid fossil discoveries is Uraraneida

(Middle Devonian to Cretaceous) (Selden et al., 2008), now interpreted as the sister group of Araneae, forming the clade Serikodiastida (Garwood and Dunlop, 2014), some depicting an odd amalgamation of characters, combining a uropygid-like pygidium and telson with spider-like fangs, spinnerets with spigots, and a highly modified palp, on the way of becoming the typical spider male instrument for sperm transfer (Huang et al., 2018; Wang et al., 2018). But what makes Uraraneida stand above all other extinct arachnid orders (i.e., Haptopoda, Phalangiotarbida, Trigonotarbida), which went extinct during the Paleozoic (Dunlop, 2010), is that they survived for at least an additional 150 million years into the Cenomanian (Cretaceous) (Huang et al., 2018; Wang et al., 2018). The case of Uraraneida highlights the importance of new fossil discoveries and the possibility that extraordinary preservation can bring to our understanding of arachnid interrelationships.

## **Final conclusions**

Reconstructing the phylogenetic relationships of Arachnida and its constituent orders remains an arduous task, yet some areas of the family tree are becoming visible among other still obscure regions. The monophyly of Arachnida continues to rely on morphology with a few recent molecular analyses finding evidence under particular sets of conditions. Within Arachnida, the clades Arachnoplumonata, Tetrapulmonata, Pedipalpi and Thelyphonida appear now well supported, virtually by all classes of data. Likewise, Parasitiformes + Opilioacarida form a clade in nearly all published analyses. However, resolving the relationships of the apulmonate arachnids will require additional data and creative analyses, as currently it is virtually impossible to place confidence on any given relationship. New fossil discoveries and the study of evodevo in new model arachnids will continue to provide additional sources of evidence to anchor some of the most unstable areas of the arachnid tree of life.

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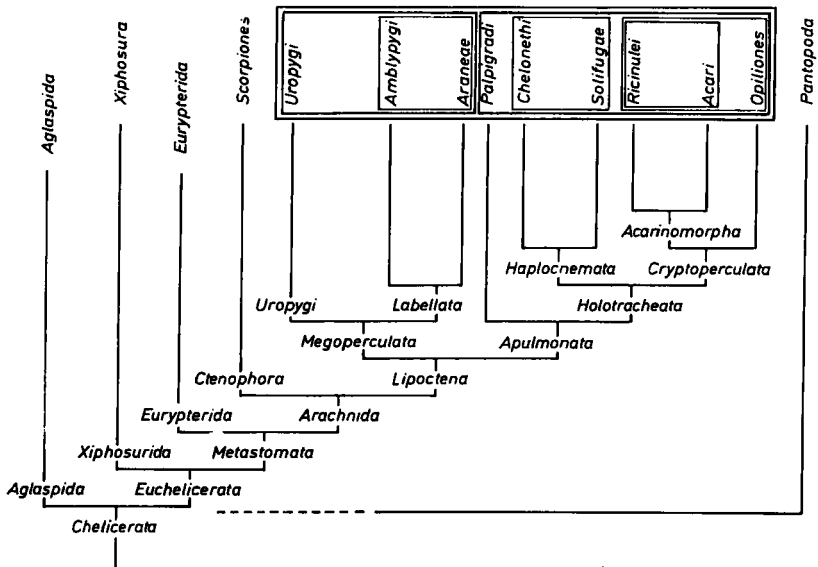
**Fig. 1.** Cladogram proposed by Weygoldt and Paulus' seminal 1979 papers on arachnid relationships.

**Fig. 2.** Selected hypotheses of arachnid relationships mostly based on morphological data or combined morphology and molecules. Notice that with the exception of Weygoldt and Paulus (1979), all other analyses place Scorpiones and Opiliones (both in bold) as either sister groups or within the same clade, a hypothesis now rejected in most molecular analyses. Instead Tetrapulmonata (extant orders in bold & oblique) are common among nearly all morphological and molecular analyses.

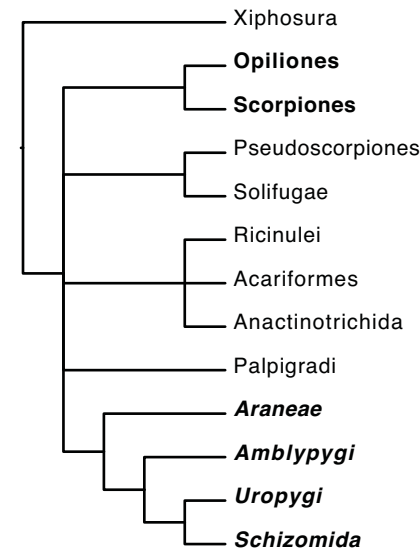
**Fig. 3.** Selected plots of bootstrap support values as genes are added in order of increasing evolutionary rate for six nodes of interest, based on Sharma et al. (2014a). Chelicerata, Euchelicerata and Arachnoplumonata show the expected trend of stabilizing with maximum support with the addition of data; Arachnida instead achieves maximum support at 500-600 genes, but the group disappears with the addition of further information; the last two plots show maximum support for conflicting sister group relationships of Ricinulei with different data matrix sizes.

**Fig. 4.** Conservative resolution of arachnid ordinal relationships including extant and fossil taxa; major clades are labelled. This is a personal view from the author and is not derived from any specific analysis.





Shultz (2007)



Garwood & Dunlop (2014), with fossils

